2 The Greater Seasonal Pool Ecosystem

The greater seasonal pool ecosystem is considerably larger than the seasonal pool itself. It extends outwards into the terrestrial landscape via biological connections and the watershed via hydrologic linkages. This section provides an overview of the variety of landscape settings and surrounding vegetative communities, explores the greater seasonal pool ecosystem, and examines the general life histories of seasonal pool-dependent fauna to elucidate the nature of their interactions with the seasonal pool ecosystem.

2.1: Setting and Vegetation of Seasonal Pools

The mid-Atlantic region is a physiographically diverse area of the United States, encompassing the extremes of the low, flat, sandy mid-Atlantic coastal plain to the greater than 5000 foot peaks of the southern Blue Ridge Mountains of Virginia. For example, Delmarva bays that are found on the Delmarva Peninsula coastal plain of Maryland and Delaware (Box 2-1) are very different physiographically as compared to the seasonal sinkhole ponds of the Shenandoah Valley of the Blue Ridge Mountains (Buhlmann et al., 1999). Seasonal pools of the mid-Atlantic reflect physiographic diversity in their wide variety of landscape settings and surrounding vegetative communities.

Seasonal pools can be found in three general landscape settings: surrounded by upland, wetland, or floodplain. Pools surrounded by upland are islands of aquatic habitat within a terrestrial landscape; pools surrounded by wetlands are part of a larger wetland complex; pools surrounded by floodplain are occasionally linked to a riverine system.

Four basic classes of seasonal pools are described below (seasonal forest pools, seasonal open-canopy pools, seasonal scrub-shrub pools, and seasonal forested wetland pools) based on their surrounding vegetative community, with short lists of common, but certainly not inclusive, species of vegetation that may be found in or around these seasonal pools (species were selected by referring to Tiner and Burke, 1995; Rawinski, 1997; Buhlmann et al., 1999; Sipple 1999; Zankel and Olivero, 1999; Colburn, 2004). Compositions of vegetative communities vary from site to site due to local environmental and historical conditions. Some pools may fall into more than one class or may not easily be placed into one. Additionally, vegetative communities are not static – they may change across the seasons and over the long-term (Tiner and Burke, 1995; Rawinski, 1997; Colburn, 2004).

Seasonal Forest Pools

Seasonal forest pools are isolated depressions surrounded by upland deciduous, mixed deciduous-coniferous, or coniferous forest (Plate 2-1). These pools may or may not be clustered in the landscape. Trees that can tolerate seasonally-saturated soils, such as white oak (*Quercus alba*), chestnut oak (*Quercus prinus*), willow oak (*Quercus phellos*), pin oak (*Quercus palustris*), American elm (*Ulmus americana*), loblolly pine (*Pinus taeda*), sweet gum (*Liquidambar styraciflua*), American beech (*Fagus grandifolia*), and sourwood (*Oxydendrum arboreum*), or trees with flood-resistant adaptations (e.g., buttresses, stilt roots) may be found around the edges of the pool depression; a few may be found in the pool itself, especially during high water levels. Seasonal forest pools are partially or completely

Photo: Lesley J. Brown

Plate 2-1. Seasonal forest pool. This seasonal forest pool is located in western Virginia.

shaded by the overhanging tree canopy but there is little or no plant growth in the pool depression itself (Tiner and Burke, 1995; Rawinski, 1997; Sipple, 1999; Colburn, 2004).

Seasonal Open-Canopy Pools

Seasonal open-canopy pools have open canopies that allow full sunlight to reach the pool (Plate 2-2). The pools may be surrounded by upland, situated within a larger wetland matrix, or in a floodplain. They may be without vegetation or may be vegetated with non-woody plant species. Emergent plants that grow in these pools may include grasses (e.g., manna grasses (*Glyceria spp.*), panic grasses (*Panicum spp.*), giant plumegrass (*Erianthus giganteus*), rice cutgrass (*Leersia oryzoides*)), sedges and rushes (e.g., sedges (*Carex spp.*), creeping rush (*Juncus repens*), woolgrass bulrush (*Scirpus cyperinus*), three-way sedge (*Dulichium arundinaceum*)), and herbs (e.g., Virginia meadow beauty (*Rhexia virginica*), marsh St. John's-wort (*Triadenum virginicum*), Virginia chain fern (*Woodwardia virginica*)).

Photo: Tim Maret

Plate 2-2. Seasonal open-canopy pool. This seasonal open-canopy pool is located in south-central Pennsylvania.

Seasonal Scrub-Shrub Pools

Seasonal scrub-shrub pools are dominated by shrubs or young trees less than 20 feet tall (6 m) growing in the seasonal pool depression (Plate 2-3). Scrub-shrub pools may be surrounded by upland forest, part of a larger wetland system, or in a floodplain. Vegetation may include common greenbrier (*Smilax rotundifolia*), highbush blueberry (*Vaccinium corymbosum*), buttonbush (*Cephalanthus occidentalis*), fetterbush (*Leucothoe racemosa*), dangleberry (*Gaylussacia frondosa*), swamp azalea (*Rhododendron viscosum*), sweet pepperbush (*Clethra alnifolia*), winterberry (*Ilex spp.*), alders (*Alnus spp.*), and water willow (*Decodon verticillatus*).

Photo: USGS PWRC

Plate 2-3. Seasonal scrub-shrub pool. This seasonal scrub-shrub pool is located at U.S. Department of Agriculture's Beltsville Agricultural Research Center, Md.

Seasonal Forested Wetland Pools

Seasonal forested wetland pools are dominated by flood-tolerant trees greater than 20 feet tall (6 m) growing in the pool basin (Plate 2-4). Seasonal forested wetland pools may be surrounded by upland forest or may be situated within a larger wetland matrix, floodplain, or oxbow of a river. Trees may include sweet gum (*Liquidambar styraciflua*), swamp black gum (*Nyssa biflora*), black gum (*Nyssa sylvatica*), laurel oak (*Quercus laurifolia*), overcup oak (*Quercus lyrata*), loblolly pine (*Pinus taeda*), red maple (*Acer rubrum*), willow oak (*Quercus phellos*), sourwood (*Oxydendrum arboreum*), water oak (*Quercus nigra*), pin oak (*Quercus palustris*), American elm (*Ulmus americana*), American holly (*Ilex opaca*), sweet bay (*Magnolia virginiana*), willows (*Salix spp.*), Atlantic white cedar (*Chamaecyperis thyoides*), and green ash (*Fraxinus pennsylvanica*).

Photo: Gary P. Fleming

Plate 2-4. Seasonal forested wetland pool. A seasonally flooded swamp forest of sweetgum (*Liquidambar styraciflua*), red maple (*Acer rubrum*), and swamp tupelo (*Nyssa biflora*). This pool is located in North Landing River Natural Area Preserve, City of Virginia Beach, Va.

Box 2-1

Example of regional seasonal pools: Delmarva bays

Delmarva bays are an example of a type of seasonal pool that is specific to an area of the mid-Atlantic region. The Delmarva Peninsula is the projection of land into the Chesapeake Bay that encompasses the entire state of Delaware and portions of Maryland and Virginia. On the Delmarva Peninsula, the landscape is pockmarked with thousands of isolated depressional wetlands or pools. These depressions are known by many names, such as Delmarva bays, Delmarva potholes, and whale wallows (Sipple, 1999). They are also sometimes categorized within the larger category of coastal plain ponds or equated with Carolina bays. 'Bay' refers to the trees that are often found in these habitats: sweet bay (*Magnolia virginiana*), red bay (*Persea borbonia*), and loblolly bay (*Gordonia lasianthus*) (Sipple, 1999). The coastal plain's relatively flat topography favors the formation of seasonal pools, fed by both groundwater and high levels of precipitation experienced in this region (Tiner, 2003a).

Delmarva bays are of variable shapes and sizes – elliptical, circular, or irregular with long-axes ranging in length from less than 305 ft to 3050 ft (100 m to 1 km) (Stolt and Rabenhorst, 1987). Their long-axes are often oriented from north to south. They generally have no standing water from midsummer to early winter. Delmarva bays may form seasonal open-canopy pools (known as 'glades') with Walter's sedge (*Carex walteriana*), giant plumegrass, twigrush (*Cladium mariscoides*), and maidencane (*Panicum hemitomon*); seasonal scrub-shrub pools with buttonbush and water willow; and seasonal forested wetland pools with red maple, sweet gum, and oaks (Sipple, 1999).

Delmarva bays are particularly abundant in the central area of the Delmarva Peninsula along the border between Maryland and Delaware, in Queen Anne's County and Caroline County in Maryland and Kent County in Delaware (Stolt and Rabenhorst, 1987). Delmarva bays' abundance over the landscape makes them important for surface water storage and helps control local flooding. During wet seasons, they serve as storage for groundwater discharge; during dry seasons, they serve as sources of groundwater recharge (Phillips and Shedlock, 1993). Delmarva bays serve as important wildlife habitat, and support many of the species described in Section 3.

2.2: Life Zones of Seasonal Pools

The seasonal pool ecosystem can be thought of as being composed of three integrated components, or life zones: the seasonal pool depression, the seasonal pool envelope (100 ft (30.5 m) radius from pool edge), and the seasonal pool terrestrial habitat (1000 ft (305 m) radius from the pool edge) (Fig. 2-1; *cf.* Semlitsch, 1998; Calhoun and Klemens, 2002; Calhoun and deMaynadier, 2004). Conceptualization of three discrete but interdependent physical areas provides insight into the overall functioning of the greater ecosystem and allows tailored conservation strategies to be developed (e.g., Calhoun and Klemens, 2002; Calhoun and deMaynadier, 2004). All three zones provide essential services that contribute to the seasonal pool ecosystem. The three seasonal pool life zones and the more prominent activities that they host are briefly described below.

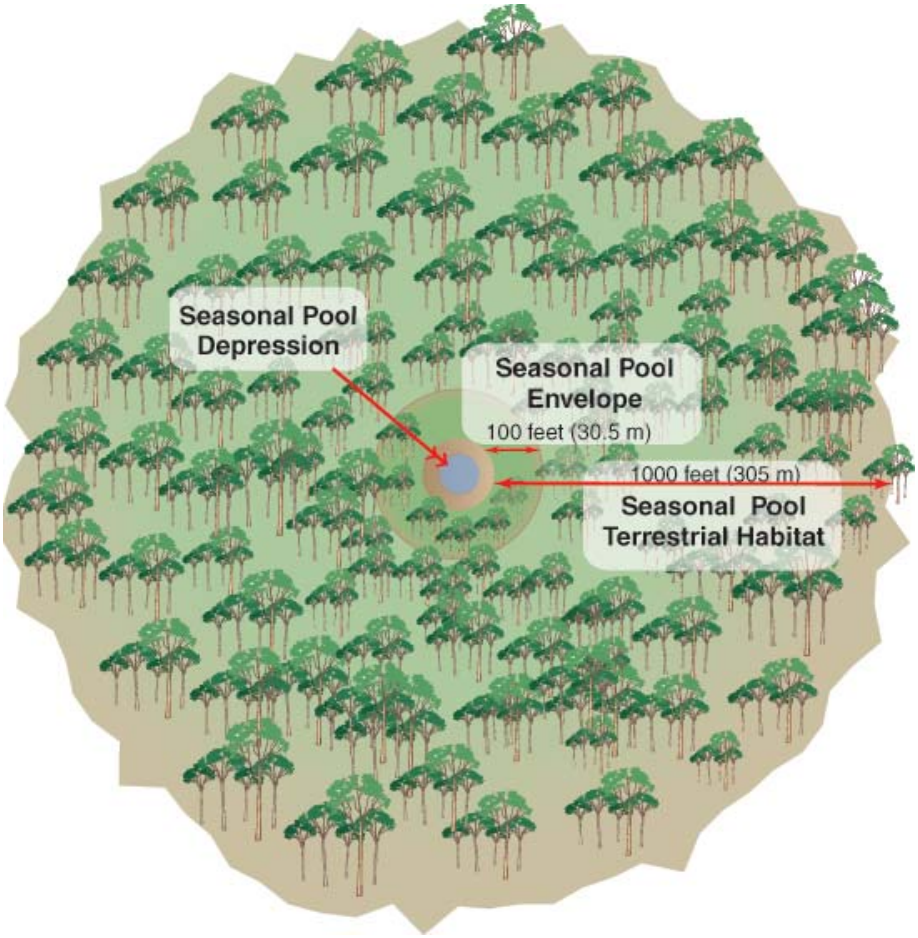

Figure 2-1. Seasonal pool aerial view delineating three life zones.* The seasonal pool depression is the entire area that fills with water during highest water levels. The seasonal pool envelope is the area immediately surrounding the pool depression, extending 100 ft † (30.5 m) beyond the edge of the depression. The seasonal pool terrestrial habitat is the area surrounding the pool that extends 1000 ft ‡ (305 m) beyond the edge of the depression (inclusive of the seasonal pool envelope).

† This width is based on the management zone designed by Calhoun and Klemens (2002).

‡ This width was determined so as to encompass the movements and habitats of pool-breeding salamanders (e.g., Semlitsch, 1998; Faccio, 2003) and to account for their high sensitivity to the amount of forest cover within this zone (e.g., Homan et al., 2004; Porej et al., 2004; Herrmann et al., 2005). However, characteristics of the landscape (e.g., forest cover, road densities) at greater distances from the pool beyond this life zone may also affect seasonal pool fauna (Homan et al., 2004; Porej et al., 2004; Herrmann et al., 2005). Additionally, juvenile wood frogs may migrate to other pools at distances significantly beyond this life zone (average of 3750 ft (1140 m); Berven and Grudzien, 1990).

* *Symbols used for diagram courtesy of the Integration and Application Network, University of Maryland Center for Environmental Science.*

Seasonal Pool Depression

The seasonal pool depression (also known as the seasonal pool basin) is the area that fills with water during highest water levels (Fig. 2-1). If there is no standing water, other visual clues may indicate the pool depression (Box 2-2; Plate 2-7). The seasonal pool depression is the epicenter of the seasonal pool ecosystem in late winter and spring, hosting amphibian breeding, amphibian egg and larval development, invertebrate life cycles, and wildlife feeding.

Amphibian Breeding. Mole salamanders (*Ambystoma spp.*) and wood frogs migrate to the seasonal pool depression from their overwintering terrestrial habitat from late winter to spring, with the exception of the marbled salamander (*Ambystoma opacum*), which migrates to the depression in the fall. The exact migration times or dates depends on the species, region, and weather. Courtship and mating takes place in the seasonal pool depression (Plate 2-5).

Photo: Steven M. Roble

Plate 2-5. Amplexus between a male and female wood frog (*Rana sylvatica*). The male wood frog clasps the female wood frog from behind while mating. There are wood frog eggs on either side of the mating pair.

Amphibian Egg and Larval Development. Depending on the species, female pool-breeding amphibians lay their eggs singly, in strings, in sheets, or as discrete masses immediately or a few days after mating (Plate 2-6). Eggs and egg masses of seasonal pool-breeders are usually attached to vegetation or woody debris below the water surface (Petranka, 1998). After hatching, salamander larvae and tadpoles develop in the pools. Salamander larvae eat zooplankton, invertebrates, and, for larger individuals, other amphibian larvae (Petranka, 1998); tadpoles primarily eat algae and detritus, although they may also eat smaller amphibian larvae and eggs.

Photo: Steven M. Roble

Plate 2-6. Release of spotted salamander eggs. These female salamanders are laying egg masses in the water of a seasonal pool.

Invertebrate Life Cycles. Seasonal pools provide habitat for a wide variety of invertebrate species. The soil at the bottom of seasonal pools may contain resting eggs from species of crustaceans, including fairy shrimp, clam shrimp, and seed shrimp, and arthropods, including caddisflies (Dodson and Frey, 1991; Hilsenhoff, 1991; Smith, 2001). Adult amphibious snails, fingernail clams, and amphipods may also survive dry conditions or overwinter by burrowing into sediments and organic debris (Smith, 2001).

Support of Terrestrial Food Webs. Invertebrates, amphibians, reptiles, birds, and mammals come to the pool depression to feed (Winfield et al., 1981; Brooks and Doyle, 2001; Kenney and Burne, 2001; Biebighauser, 2002; Colburn, 2004). Amphibian egg masses, invertebrate and amphibian larvae, and emerging insects and amphibians provide a significant food source for visiting predators. Seasonal pools serve as important feeding and watering sites for wetland- or aquatic-dependent animals traveling across the landscape.

Box 2-2
Recognizing dry seasonal pools*

If there is no standing water, other visual clues can be used to identify seasonal pools that fill with water in another season.

Characteristic Topography
- Depressions in otherwise flat topography
- "Pit-and-mound" topography

Clues from Seasonal Pool Biota
- Fingernail clams and clam shells
- Caddisfly cases
- Snails and snail shells
- Fairy shrimp eggs

Evidence of Water
- Stained or sediment-covered leaves
- Trees with flood-resistant adaptations (e.g., buttresses, stilt roots)
- Sphagnum moss, ferns
- Wetland plants growing in dry soil
- Wetland (hydric) soils
- Water stains on trees

** Colburn, 1997; Tappan, 1997; Calhoun, 2003*

Photo: USGS PWRC

Plate 2-7. Recognizing dry seasonal pools. Water stains at the base of trees presents evidence that this area fills with water. This seasonal pool is located at the Patuxent Research Refuge, Laurel, Maryland.

Seasonal Pool Envelope

The seasonal pool envelope is the terrestrial habitat immediately surrounding the pool; it is a management zone that extends approximately 100 feet (30.5 m) from the pool edge (Fig. 2-1; Calhoun and Klemens, 2002; Calhoun and deMaynadier, 2004). This area supports activities related to amphibian breeding, provides terrestrial habitat to juvenile and adult amphibians, and plays a large role in regulating water quality.

Amphibian Breeding. During the amphibian breeding season (from late winter to spring for most species), high densities of adult amphibians may occupy the seasonal pool envelope (Plate 2-8; Calhoun and Klemens, 2002). They spend their days hidden in this area near the edge of the seasonal pool or in the pool itself, and their nights in the pool engaged in breeding activities. Male amphibians may arrive up to several days or weeks earlier than females and wait for females to arrive in this area (Bishop, 1941; Shoop, 1960; Semlitsch, 1981). Marbled salamanders, unlike the other species in the mole salamander family, breed in the late summer or fall and may mate in the seasonal pool envelope. Male marbled salamanders often intercept females en route to the breeding pools, and initiate courtship in the pool envelope before the females reach the pool depression (Bishop, 1941; Krenz and Scott, 1994).

Photo: USGS PWRC

Plate 2-8. Spotted salamanders at pool edge. These salamanders are spending their daylight hours during the breeding season under a cover object in the mud at the margin of a seasonal pool.

Juvenile and Adult Amphibian Habitat. From summer to fall, the seasonal pool envelope is occupied by large numbers of recently metamorphosed juvenile frogs and salamanders. They may burrow into the mud near the pool edge or hide beneath rocks and logs to survive dry weather before making their emigration from the pools to their overwintering habitat (Richmond, 1947; Shoop, 1974). Wintering juvenile and adult wood frogs occur in greatest densities within 30 m of pools and are highly sensitive to disturbances in this area (Homan et al., 2004; Regosin et al., 2005).

Water Quality. The seasonal pool envelope plays a large role in regulating seasonal pool water quality. Soil buffers run-off and snowmelt before it enters the pool (Gascon and Planas, 1986). Vegetation (tree roots and ground cover) traps sediment before it enters the pool. Overhanging vegetation regulates pool temperature and supplies organic material to the pool depression; leaf litter serves as food for fungi, bacteria, and invertebrates (Colburn, 2004). Vegetation also influences a pool's hydrologic regime – trees and shrubs withdraw water from the pools, especially in the spring and summer.

Seasonal Pool Terrestrial Habitat

Seasonal pool terrestrial habitat is the area that extends 1000 ft (305 m) from the edge of the seasonal pool depression (Fig. 2-1). The portion of this life zone that remains forested or unimpacted by human activities provides habitat to pool-breeding amphibians and other wildlife, serves as a terrestrial corridor between pools, and plays a role in regulating water quality.

This management zone encompasses the habitat of over 95% of populations of pool-breeding salamanders (Semlitsch, 1998; Faccio, 2003), although this area is not sufficient to encompass all movements of seasonal pool-breeding amphibians (e.g., juvenile wood frog migrations, Berven and Grudzien, 1990). Also, the seasonal pool biological community may be influenced by characteristics of the landscape (e.g., amount of forest cover, densities of roads) well beyond the seasonal pool terrestrial habitat zone (Homan et al., 2004; Porej et al., 2004).

Amphibian and Other Wildlife Habitat. Seasonal pool-breeding amphibians of the mid-Atlantic region spend approximately 90% of their juvenile and adult lives in the terrestrial landscape (Semlitsch, 1998), and exhibit seasonal variation in terrestrial habitat use. During the winter, wood frogs find shelter and hibernate in upland forests; during their more active period, they forage and find shelter in moist lowland forests (Hulse et al., 2001; Regosin et al., 2003b). Spotted salamanders may occur at uniform densities up to and exceeding 984 ft (300 m) away from seasonal pools (Homan et al., 2004). Seasonal pool-breeding amphibians play important roles in forest ecology, as prey for wildlife and as predators of invertebrates. In a given area of forest, they may comprise a higher biomass than the breeding birds and small mammals combined (Windmiller, 1996). Many other species of wildlife inhabit the seasonal pool terrestrial habitat, including snakes, turtles, birds, and terrestrial amphibians. They feed on the resources produced in the seasonal pool (Winfield et al., 1981; Brooks and Doyle, 2001; Kenney and Burne, 2001; Biebighauser, 2002; Colburn, 2004).

Biological Corridor. The terrestrial forested habitat functions as a biological corridor, whereby animals can travel between pools. Pool-breeding amphibians and other animals may disperse from one pool to another.

Water Quality. The water quality of the pool will be determined by the entire watershed, which will extend into the seasonal pool terrestrial habitat and possibly even farther, depending upon the characteristics of the watershed and the source of the water.

2.3: Life Histories of Seasonal Pool-Dependent Organisms

Seasonal pool-dependent animals have developed behavioral (e.g., effective immigration and emigration strategies), physiological, or structural adaptations that allow them to survive and/or reproduce in the highly dynamic environment of seasonal pools (Wiggins et al., 1980; Williams, 1987). Seasonal pool-dependent animals may be classified into three general life history classes: migratory breeders, non-breeding migrants, and permanent residents (based on Colburn, 2004; builds upon and modifies previous classification systems of Wiggins et al., 1980; Williams, 1987). This classification system is presented below, in the context of mid-Atlantic seasonal pools.

Migratory Breeders

"Migratory breeders" are those animals that breed in seasonal pool depressions during the flooded phase and vacate pools during the dry phase (Colburn, 2004). The most visible members of this life history grouping are pool-breeding amphibians (Box 2-3; see Section 3 for more information).

Besides amphibians, some invertebrate species rely on this life history strategy as well. Limnephilid caddisfly adults spend summers in caves and tree holes and return to the pools to breed (Colburn, 2004). Certain species of predaceous diving beetles, backswimmers, and water boatman spend portions of their life cycles in permanent water bodies away from seasonal pools (Colburn, 2004).

Box 2-3
Life history of pool-breeding amphibians

Amphibian migratory breeders have biphasic life cycles, requiring both aquatic and terrestrial habitats (Semlitsch, 1998, 2003). Early stages of development are spent as eggs and larvae in seasonal pools. The transition from an aquatic to a terrestrial life stage occurs at metamorphosis, when amphibians emerge from their natal pools and enter the terrestrial habitat.

As adults, they return to seasonal pools from their terrestrial habitats to breed. Once having bred in a particular pool, adult wood frogs have been found to be very faithful to their pools (Berven and Grudzien, 1990). There is evidence that other pool-breeding amphibians exhibit similar levels of breeding pool fidelity (e.g., *Ambystoma maculatum*, Scott, 1994) returning to the same pools and following the same migration paths. Males arrive at breeding pools earlier and stay later than females (Bishop, 1941; Shoop, 1960; Semlitsch, 1981).

Dispersal between local populations occurs when animals breed in pools other than their natal pools. Dispersal in wood frogs and other seasonal pool-breeding amphibians is age-specific, with juveniles accounting for most or all of the movements between ponds (Berven and Grudzien, 1990). Wood frogs may emigrate more than 3750 ft (1140 m) from their natal pools to breed as adults in other pools (Berven and Grudzien, 1990).

The behavior and habitat requirements of the terrestrial stage of pool-breeding amphibians are not fully understood, primarily due to the logistical difficulties in their study and the amphibians' nocturnal and belowground habits (Petranka, 1998; Dodd and Smith, 2003; Semlitsch, 2003). Pool-breeding amphibians must keep their skin cool and moist. Thus microclimates play a large role in the suitability of a particular habitat for amphibians (Gibbs, 1998; Guerry and Hunter, 2002); mature forests provide appropriate microclimates (Semlitsch, 1981; Petranka et al., 1994; deMaynadier and Hunter, 1999; Rothermel and Semlitsch, 2002; Faccio, 2003). Mole salamanders require sufficient belowground refugia, which provide protection from predators and freezing temperatures (Madison, 1997; Regosin et al., 2003a). Mole salamanders may emigrate more than 650 ft (200 m) from their breeding pools to their terrestrial habitat (Semlitsch, 1981; Madison, 1997). Females of pool-breeding amphibian populations are more likely to overwinter at greater distances away from pools compared to males (Regosin et al., 2003a, b).

Non-Breeding Migrants

"Non-breeding migrants" are those animals that migrate to seasonal pools for feeding, rather than breeding, a behavioral adaptation used to exploit seasonal pool resources (Williams, 1987; Colburn, 2004). This group may include species of predaceous diving beetles, turtles, snakes, birds, and mammals. Freshwater turtles that frequent seasonal pools generally feed on algae, terrestrial and aquatic plants, and invertebrates. Snakes that have aquatic or semi-aquatic life histories, such as the ribbonsnake, may hunt for amphibians in the water of a seasonal pool. Birds and mammals use seasonal pools as sources of water and food (see Section 3).

Permanent Residents

"Permanent residents" are those animals that do not spend significant amounts of time away from the seasonal pool (Colburn, 2004). Permanent residents are those with unique physiological and behavioral adaptations to withstand drying and extreme temperature changes. Some beetles, fingernail clams, and other invertebrates spend the dry phase or winter season aestivating in the sediment of pool depressions. One of the most distinctive inhabitants of some seasonal pools, fairy shrimp, as well as species of flatworms, mosquitoes, and beetles, survive pool drying as drought-resistant eggs or cysts that hatch upon flooding (Smith, 2001). This life history group also includes insects that spend their larval stages in seasonal pools and become aerial as adults but do not travel far from pools (Colburn, 2004).